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The relationship between forage cell wall content and voluntary food intake in mammalian herbivores

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"Der Zusammenhang zwischen dem Gehalt an Zellwandbestandteilen und der freiwilligen Futteraufnahme bei pflanzenfressenden Säugetieren"

Man geht davon aus, dass Tiere eine sinkende Futterqualität durch erhöhte Futteraufnahme kompensieren. Unterschiede in der Reaktion auf sinkende Futterqualität wurden insbesondere zwischen Rindern (Wiederkäuern) und Pferden (Dickdarmfermentierern) postuliert. Diese Hypothesen wurden anhand einer Sammlung von Daten aus der Literatur überprüft. Nur bei kleinen Nagetieren, und möglicherweise bei Kaninchen, war ein Anstieg der Futteraufnahme bei Raufuttern steigenden Fasergehalts zu verzeichnen. Insbesondere zeigten große Pflanzenfresser, auch Pferde, das Muster einer sinkenden Futteraufnahme bei steigendem Fasergehalt - wie bei Hauswiederkäuern beschrieben. Die verfügbaren Daten stützen die Annahme nicht, dass die Futteraufnahme bei sinkender Futterqualität ansteigt. Stattdessen ergibt sich die Vermutung, dass große Pflanzenfresser meist eine antizipierende Futteraufnahme-Strategie anwenden, bei der in Zeiten der Verfügbarkeit hochwertiger Äsung Körperreserven angelegt, und in Zeiten minderwertiger Äsung die Futteraufnahme (und potenziell die metabolischen Verluste) reduziert werden. Wir stellen die Hypothese auf, dass ein Separationsmechanismus im Kolon, der zur Verringerung der metabolischen Kotverluste mit Koprophagie gekoppelt ist, unterhalb einer gewissen Körpergröße notwendig ist, unter der eine antizipierende Strategie nicht möglich ist. Zukünftige Untersuchungen, die feine Unterschiede untersuchen wollen, sollten nicht-domestizierte Tierarten nutzen.

The relationship of forage cell wall content and voluntary food intake in mammalian herbivores

It is generally assumed that animals compensate a decrease of diet quality by an increase of diet intake. Differences in the reaction to a decrease in diet quality have been proposed particularly between cattle (ruminants) and horses (hindgut fermenters). These hypotheses were tested with a literature data collection. Only in rodents, and potentially in lagomorphs, was an increase in food intake with increasing diet fibre content evident. Large herbivores, including horses, show a decreased food intake as diet fibre content, similar to the pattern known in domestic ruminants. The available data do not support the hypothesis that increasing food intake compensates for decreasing diet quality. Instead, the hypothesis results that large herbivores practice an anticipatory feeding strategy, accreting body reserves in times of high diet quality and reducing intake on low quality food (potentially to minimize metabolic losses). We propose that beyond a certain body size, beyond which body reserve accretion is not possible in sufficient scope, a colonic separation mechanism coupled with caecotrophy is necessary to minimize metabolic losses at high intakes. Future studies aiming at determining differences between herbivore groups should focus on non-domestic species.

REVIEW

The relationship between forage cell wall content and voluntary food intake in mammalian herbivores

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ABSTRACT

1. It is generally assumed that animals compensate for a declining diet quality with increasing food intake. Differences in the response to decreasing forage quality in herbivores have been postulated particularly between cattle (ruminants) and horses (hindgut fermenters). However, empirical tests for both assumptions in herbivorous mammals are rare.

2. We collected data on voluntary food intake in mammals on forage-only diets and related this to dietary neutral detergent fibre (NDF) content, assuming a nonlinear correlation between these measurements. Generally, the paucity of corresponding data is striking.

3. Elephants and pandas showed very high food intakes that appeared unrelated to dietary fibre content. Only in small rodents, and possibly in rabbits, was an increase in food intake on forages of higher NDF content evident. In particular, other large herbivores, including horses, followed patterns of decreasing intake with increasing forage NDF, also observed in domestic cattle or sheep.

4. For large herbivores, empirical data therefore do not – so far – support the notion that intake is increased in response to declining diet quality. However, data are in accord with the assumption that most large herbivores have an anticipatory strategy of acquiring body reserves when high-quality forage is available, and reducing food intake (and potentially metabolic losses) when only low-quality forage is available.

5. Intake studies in which the influence of digestive strategy on food intake capacity is tested should be designed as long-term studies that outlast an anticipatory strategy and force animals to ingest as much as possible.

6. We suggest that a colonic separation mechanism coupled with coprophagy, in order to minimize metabolic faecal losses, is necessary below a body size threshold where an anticipatory strategy (living off body reserves, migration) is not feasible. Future studies aimed at investigating fine-scale differences, for example between equids and bovids, should focus on non-domesticated species.

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Keywords: diet quality, foregut fermenter, herbivory, hindgut fermenter, seasonality

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INTRODUCTION

Animals ingest food to meet their requirements for energy and nutrients. A common concept of voluntary food intake in animals is that with increasing energy (or nutrient) density in the diet (generally referred to as 'diet quality'), animals ingest less of this diet because their requirements are met by smaller amounts. In reverse, this implies that as diet quality decreases, animals ingest more of the diet (Karasov & Martínez del Rio, 2007; Barboza et al. 2009). We term this the 'instantaneous response' strategy.

This fundamental strategy has been demonstrated in numerous feeding trials with mammals such as rodents (Peterson & Baumgardt 1971, Kanarek et al. 1977, del Valle et al. 2006), rabbits *Oryctolagus cuniculus* (Cheeke 1987), marsupials (Wellard & Hume 1981), pigs (Owen & Ridgman 1968), primates (Edwards & Ullrey 1999a, 1999b), horses *Equus ferus caballus* (Laut et al. 1985) or ruminants (Dinius & Baumgardt 1970, Baer et al. 1985, Schwartz et al. 1988a, Plowman 2002). These feeding trials are all performed with artificial feeds, mostly pelleted compound feeds, in which grain products were the main energy-supplying component, and varying levels of fibrous substrates are added to achieve different caloric densities. By intuition, it is assumed that this strategy also determines the voluntary food intake of herbivores on natural forages (e.g. Karasov & Martínez del Rio, 2007), but this concept has hardly ever been tested empirically.

Several considerations make this strategy less self-evident than it might at first appear. On the one hand, the use of artificial compound feeds hardly reflects characteristics of actual forages in the wild: whereas the digestibility of the high-energy ingredients of compound feeds can be assumed to remain constant irrespective of the degree of dilution with fibrous ingredients, the digestibility of the more nutritious components of whole forages cannot be expected, similarly, to retain a high level as the fibrousness of the whole forage increases. In other words, whereas it might pay to increase intake on diluted compound feeds, this might be less rewarding on real forages of decreasing quality. On the other hand, empirical data on voluntary food intake in herbivores fed whole forages contradict the concept of instantaneously compensating food intake, for example when comparing voluntary intake in zoo herbivores fed two different roughages of different nutritional quality (Foose 1982; Fig. 1). It appears that these animals rather followed an 'anticipatory response' strategy. Actually, the experience that herbivores decrease their food intake with decreasing forage quality is common knowledge in applied agricultural science (Van Soest 1994, pp. 342–344) – but with respect to herbivores, this research area is evidently limited to ruminants only.

Can herbivores actually adjust their voluntary food intake in order to compensate for a lower dietary quality of forage available to them? Our concept of this question has been influenced enormously by a presumed dichotomy between two herbivore groups – the equids and the ruminants. Based on hypotheses put forward by Bell (1971), Janis (1976) and Foose (1982), it is commonly assumed that ruminants, on the one hand, are increasingly limited in their food intake capacity as diet quality decreases, and have a typical drop in intake with increasing fibre content (Cordova

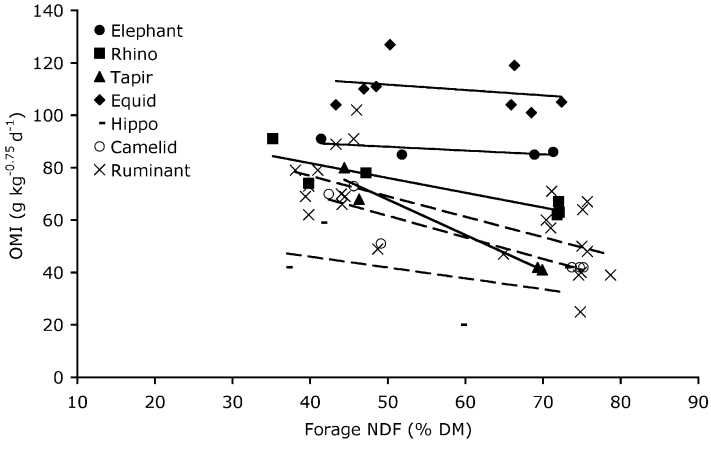


Fig. 1. The relationship of forage fibre content (measured as neutral detergent fibre, NDF, in dry matter) and voluntary food intake (measured as organic matter intake, OMI) in different captive wild herbivores (from Foose 1982). Regression lines for hindgut fermenters (solid lines) and foregut fermenters (dashed lines) are shown. Note that food intake invariably decreases with increasing fibre content for each group, although to different degrees. Steep declines are not restricted to ruminants or foregut fermenters, but also occur in the hindgut fermenting rhinoceroses and tapirs.

et al. 1978, Meissner & Paulsmeier 1995). This is assumedly caused by a mechanical intake limitation, where more fibrous food has to be ruminated upon for a longer time before it can clear the rumen. In contrast, horses are assumed to be either 'less affected' by an increase in dietary fibre or capable of even 'compensatory increasing intake' on higher-fibre forage, due to the absence of a similar mechanical constraint. In other words, equids are assumed to function as one would expect any herbivore to function (a decrease in diet quality is instantaneously compensated by an increase in intake), whereas ruminants are considered peculiar, due to their passage-delaying, and hence intake-compromising, forestomach physiology. This general concept was summarized by Janis (1976) in an eye-catching figure (Fig. 2).

A closer look at the original text (Janis 1976, p. 764) shows that the author herself noted that experimental data on horses fed various roughages also showed a decrease in food intake as forage quality declined. Nevertheless, maybe due to the convincing simplicity of the figure, the theory that horses do compensate for declining diet quality by increasing intake has found its way into reviews and textbooks of animal physiology (Hume & Warner 1980, Van Soest 1996, von Engelhardt & Breves 2005). Individual studies, however, could not substantiate this presumed difference between ruminants and equids. For example, Cymbaluk (1990; Fig. 3) hardly found any difference in the voluntary forage ingestion between cattle *Bos primigenius taurus* and horses, and Pearson et al. (2006) similarly noted a parallel decrease in food intake with increasing roughage fibre level in ponies and domestic ruminants. Actually, the notorious difficulty of making domestic horses accept straw-only diets (Vernet et al. 1995, Dulphy et al. 1997b, Kienzle et al. 2002) appears to contradict the notion that they are particularly adapted to forages of low nutritional quality.

Foose (1982) tested experimentally whether different large mammalian herbivores reacted in different ways to two different forages (grass and lucerne hay, Fig. 1).

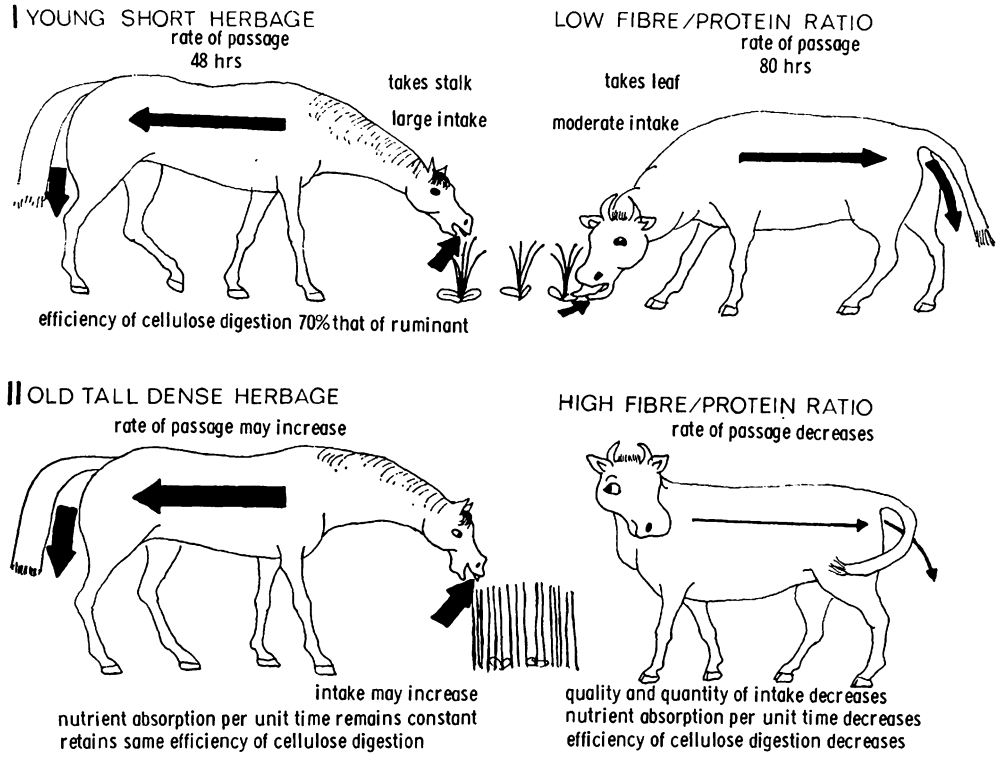


Fig. 2. Graphic summary of the juxtaposition of equids and ruminants from Janis (1976). Equids are hypothesized to be able to increase forage intake compensatorily as forage quality declines.

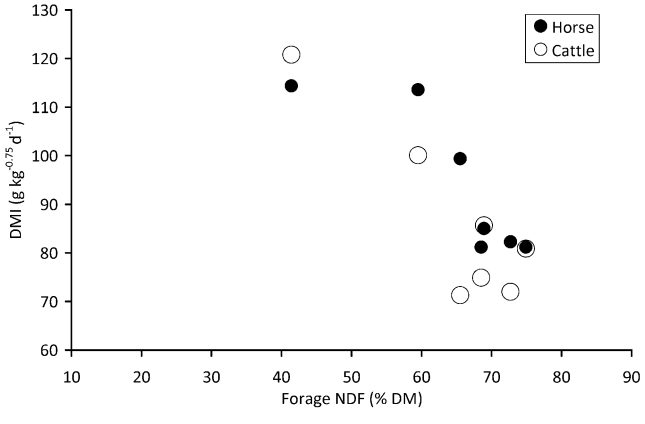


Fig. 3. Comparative voluntary dry matter intake (DMI) of horses and cattle on roughages of different neutral detergent fibre (NDF) content (Cymbaluk 1990).

Differences in the level of food intake, and in the degree of food intake reduction, were evident between certain groups (compare, for example, the slopes for equids and elephants to those of ruminants or camelids in Fig. 1), but other groups, such as rhinoceroses or tapirs, showed a similar pattern to that of the ruminants, in spite of

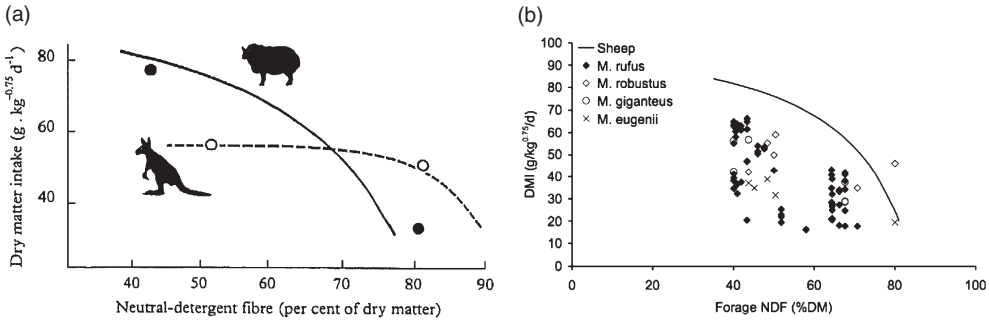


Fig. 4. Relationship between forage neutral detergent fibre (NDF) content and voluntary dry matter intake (DMI) in sheep and macropods: (a) as suggested by Hume (1999, 2002), using data from Hollis (1984) for macropods and Van Soest (1965) for sheep; (b) empirical data collection from Munn et al. (2008) for macropods and Van Soest (1965) for sheep.

the similarity of their digestive anatomy to that of equids. However, while these data might not be considered sufficient to test a difference between these individual herbivore groups, the one most striking, yet rarely emphasized, result of these studies, is that nearly every species investigated showed a higher food intake of the forage with the lower fibre content, in evident contrast to the concept of compensatory intake.

The concept of Janis (1976) that ruminants are more intake-limited than horses was additionally transferred to the comparison of ruminants and macropods (kangaroos); because the macropod forestomach resembles the equid hindgut in its macroscopic anatomy, and because macropods do not ruminate, it was concluded that macropods should be similarly unconstrained in their food intake as horses, and should show less decline in food intake with increasing dietary fibre content than ruminants (Hume 1999). An according graphical depiction of the relationship between dietary fibre and voluntary food intake in sheep and macropods has found widespread distribution (Hume 1999, 2002; Fig. 4a); however, a complete collection of empirical data does not support a fundamental difference between sheep and macropods in this respect (Munn et al. 2008; Fig. 4b).

In this review, we tested whether published empirical data indicate that

1. herbivores compensate for declining food quality (measured as fibre content) by increasing voluntary food intake, and

2. fundamental differences exist in the degree that dietary fibre content influences voluntary food intake between various herbivore groups.

METHODS

We screened the scientific literature for food intake studies in herbivorous mammals. The literature research was conducted using the search engines 'Google Scholar', 'Pubmed' and 'Zoological Records' of the library of the University of Zurich, Switzerland. Subsequently, the reference lists of publications thus acquired, and of standard textbooks (Robbins 1993, Van Soest 1994, Hume 1999; Karasov & Martínez del Rio, 2007; Barboza et al. 2009), were screened for further sources. Only studies were chosen in which (i) intake was recorded in dry matter (or could be calculated from the available data in dry matter); (ii) natural forages (mostly hay, or browse or other

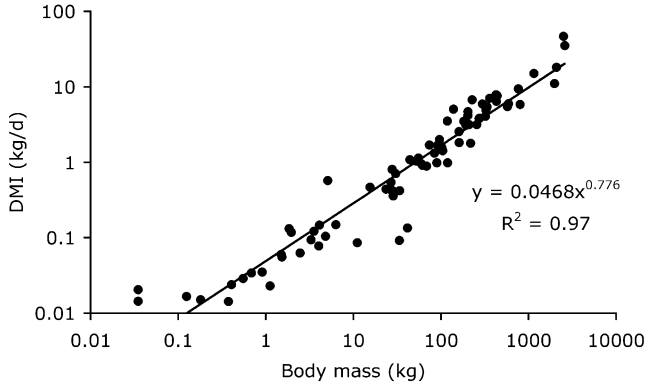


Fig. 5. Allometric relationship between body mass and absolute dry matter intake (DMI) in the 84 mammalian herbivore species investigated in this review (one average value per species).

natural plant parts) were used; (iii) a measure of dietary fibre content (neutral detergent fibre NDF, acid detergent fibre ADF, or crude fibre CF) was given; (iv) food was offered *ad libitum*; and (v) the body mass of the animals was recorded or the food intake was given per unit metabolic body weight ($BM^{0.75}$).

Dry matter intake (DMI) was expressed per unit metabolic body weight ($BM^{0.75}$). This was done for several reasons. As reviewed by Clauss et al. (2007), food intake in mammals is scaled to body mass with an exponent of approximately 0.75 in various datasets. Therefore, several studies also included in this analysis give intake data as based on $BM^{0.75}$ (Van Soest 1965, Reid et al. 1988). In the data collection of this study, a regression of species' averages for body mass and absolute dry matter intake (kg/d; calculated as ln-transformed data, linear regression, by SPSS 16.0, SPSS Inc., Chicago, IL, USA) for which absolute intake and body mass were given, yielded a relationship of DMI (kg/d) = $0.0468\ BM^{0.776}$ with a 95% confidence interval for the exponent of 0.730–0.822 (Fig. 5).

In cases where the NDF content was not given for the diets used, but either ADF or CF was available, we followed the approach of Munn et al. (2008) and calculated (a) for grass, grass hay or straw (Anonymous 2001):

$$\text{NDF (\%DM)} = 2\ \text{ADF (\%DM)} - 13.78$$

(b) for lucerne, clover or other legumes (Anonymous 2001):

$$\text{NDF (\%DM)} = 1.22\ \text{ADF (\%DM)} + 0.89$$

and (c) if crude fibre (CF) was recorded (Kamphues et al. 2004):

$$\text{NDF (g/kgDM)} = 1.58\ \text{CF (g/kg DM)} + 135.7$$

An important question when comparing voluntary intake to fibre content of the diet is: what kind of relationship is assumed? In many studies, the relationship is investigated by using linear regressions, which means that for different forage classes (e.g. legumes, C3 grasses, C4 grasses) different regressions must be calculated (Reid et al. 1988, Lawrence et al. 2001). However, if one axis contains a proportional measurement (here: NDF content in %DM), a linear regression means that some equations allow a theoretical extrapolation beyond biological values (here: NDF of >100% DM). Here, we follow the approach of Van Soest (1965) who, using a dataset from 83 intake trials in sheep, found a correlation between DMI and dietary NDF of

$$\text{DMI}\,(\text{g kg}^{-0.75}\text{d}^{-1}) = 110.4 - (1716/(100 - \text{NDF}))$$

The resulting equation tends towards infinitely negative values as NDF approaches 100%. Using TableCurve 2D v5.01 (Systat Software UK Ltd, London, UK), the equation

$$y = a - (b/(100 - x))$$

was fitted to the datasets assembled in this study, and 95% confidence intervals (CI) were determined for *a* and *b*. Results are displayed graphically in comparison to the original Van Soest (1965) equation.

RESULTS

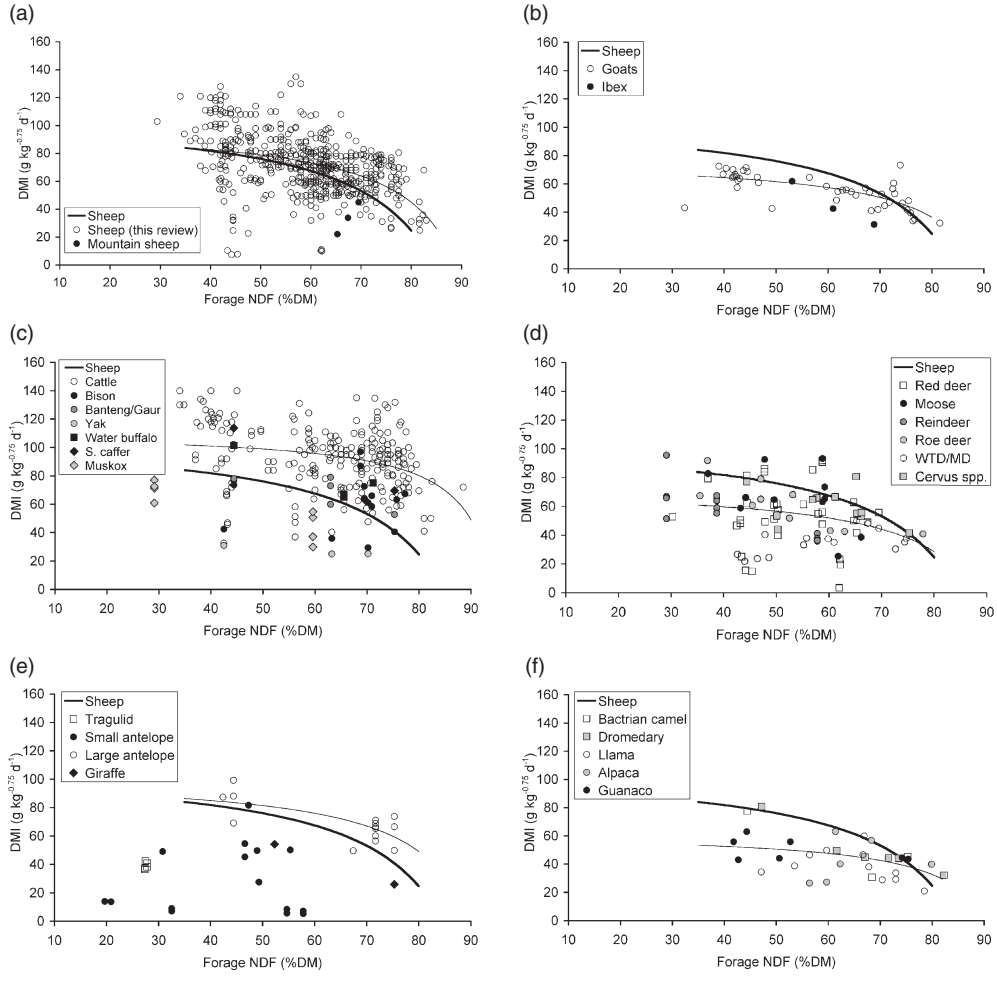
We included in this review data from 122 publications that documented feeding trials in which roughages were fed to 84 species of mammalian herbivore on an *ad libitum* basis. Of the 122 publications, only three documented animals actually increasing their food intake on the diet with the higher fibre content. These were one publication on horses (Pearson et al. 1992), one on voles *Microtus* spp. (Young Owl & Batzli 1998), and one on pocket gophers *Thonomys bottae* (Loeb et al. 1991). In all other cases, either only one roughage diet was included in the experimental design, or voluntary intake of roughages declined with increasing fibre content.

For many mammalian groups or species, there were not enough data points to yield significant regression equations; significant equations are listed in Table 1.

The data collected for domestic sheep *Ovis aries* yielded a similar, yet slightly higher curve than the one found by Van Soest (1965; from now on called 'sheep standard'; Fig. 6a). Data for domestic goats *Capra aegagrus hircus* also gave a good fit to the 'sheep standard' (Fig. 6b), but the lack of overlap of the 95% confidence interval (CI) for *a* indicates a generally lower intake than that of domestic sheep in this collection (Table 1). Voluntary intake in domestic cattle was generally higher than in sheep or goats and yielded a curve distinctively elevated compared to the

Table 1. Regression equations for the relationship between dietary fibre content (measured as neutral detergent fibre, NDF in % dry matter) and voluntary dry matter intake (DMI) according to DMI = a – (b/(100 – NDF)) in mammalian herbivores. 'Sheep standard' from Van Soest (1965)

Herbivore group	*a*	(95% CI)	*P*	*b*	(95% CI)	*P*	R^2
'Sheep standard'	110.4	–	–	1716	–	–	
Sheep	101.5	(95.8–107.2)	<0.001	1129	(923–1335)	<0.001	0.19
Goat	78.3	(71.3–85.3)	<0.001	837	(602–1073)	<0.001	0.53
Cattle	111.4	(102.6–120.2)	<0.001	624	(349–899)	<0.001	0.08
Cervids (all)	75.3	(61.3–89.3)	<0.001	933	(340–1527)	0.002	0.09
Reindeer	116.2	(91.3–141.1)	<0.001	3329	(1992–4666)	<0.001	0.69
Roe deer	91.5	(64.1–118.9)	<0.001	1337	(204–2471)	0.026	0.48
Large antelope	102.9	(79.8–126.0)	<0.001	1074	(359–1790)	0.007	0.47
Camelids (all)	62.5	(50.2–74.8)	<0.001	597	(214–980)	0.003	0.22
Large camels	82.8	(61.5–104.2)	<0.001	1018	(436–1600)	0.003	0.60
Horse	105.6	(88.7–122.5)	<0.001	647	(120–1173)	0.017	0.08
Donkey	98.4	(86.6–110.2)	<0.001	670	(433–961)	<0.001	0.63
Rhinos (all)	108.8	(88.6–129.0)	<0.001	1457	(807–2108)	<0.001	0.48
White rhino	97.0	(70.1–123.9)	<0.001	1186	(360–2012)	0.008	0.38
Macropods (all)	66.0	(56.9–75.1)	<0.001	1099	(715–1483)	<0.001	0.29
Macropus rufus	77.3	(63.8–90.7)	<0.001	1670	(1095–2245)	<0.001	0.38



sheep standard (Fig. 6c), with minimal overlap of the 95% CI for *a* in the domestic sheep and cattle (Table 1). Wild sheep, wild goats, wild cattle and muskoxen *Ovibos moschatus* showed intakes at the lower end of the respective range of the domestic species (Fig. 6a–c). Cervids in general showed intakes in the range of domestic sheep (95% CI overlap for *a* and *b*, Table 1; Fig. 6d), but again on the lower side of the range. The very limited data on tragulids, small antelopes and giraffe *Giraffa camelopardalis* showed intakes in the lower range of that of domestic sheep or below, whereas large antelope closely fitted the sheep regression line (Table 1; Fig. 6e). Camelids again showed intakes in the lower range of that of domestic sheep (Fig. 6f), and there was no overlap between domestic sheep in this study and all camelids combined (Table 1).

Domestic horses showed a similar pattern to domestic cattle (Fig. 7a), and values for *a* and *b* were very similar between these two species (Table 1). Horses were closer to domestic cattle than to the 'sheep standard'. The few existing measurements for wild equids were in the upper range of domestic horse values (Fig. 7a). Domestic donkeys *Equus africanus asinus* had intakes between the 'sheep standard' and the regression line for domestic cattle of this study (Fig. 7b), but with a lower *b* than

Fig. 6. Relationship between forage neutral detergent fibre (NDF) content and voluntary dry matter intake (DMI) in (a) domestic and wild sheep (Foot & Romberg 1965, Haenlein et al. 1966, McIntosh 1966, Leaver et al. 1969, Forbes & Tribe 1970, Sutton & Vetter 1971, Jones et al. 1972, Hume 1974, Sharma & Rajora 1977, Miles et al. 1978, Milne et al. 1978, Dellow & Hume 1982, Foose 1982, Varga & Prigge 1982, Aitchison et al. 1986, Baker & Hobbs 1987, Reid et al. 1988, Gihad et al. 1989, Warmington et al. 1989, Domingue et al. 1991, Lemosquet et al. 1996, Vernet et al. 1996, Dulphy et al. 1997a, Dulphy et al. 1997b, 1997c, Fraser & Baker 1998, Burns et al. 2005, Pearson et al. 2006, Burns et al. 2007, Schlecht et al. 2007), (b) domestic goats (Jones et al. 1972, Sharma & Rajora 1977, Chosniak et al. 1984, Gihad et al. 1989, Domingue et al. 1991, Oosting & Waanders 1993, Sponheimer et al. 2002, Coleman et al. 2003, Burns et al. 2005, Burns et al. 2007, Schlecht et al. 2007), (c) domestic and wild cattle (Haenlein et al. 1966, Kowalczyk et al. 1976, Richmond et al. 1977, Sharma & Rajora 1977, Hawley et al. 1981, Foose 1982, Williams & Dudziński 1982, Prigge et al. 1984, Reid et al. 1988, Cymbaluk 1990, Prigge et al. 1990, Renecker & Hudson 1990, Galloway et al. 1991, Goetsch et al. 1991, Galloway et al. 1992, Forster et al. 1993, Galloway et al. 1993, Prigge et al. 1993, Burns et al. 2005, Pearson et al. 2006, Burns et al. 2007, Schlecht et al. 2007, Bhatti et al. 2008, Schwarm et al. 2009, Lechner et al. 2010), (d) cervids (WTD white tailed deer, MD mule deer) (Ullrey et al. 1971; Drożdż & Osiecki 1973; Mautz et al. 1976, Milne et al. 1978, Foose 1982, Baker & Hansen 1985, Baker & Hobbs 1987, Schwartz et al. 1988b, Renecker & Hudson 1990, Domingue et al. 1991, Sibbald & Milne 1993, Freudenberger et al. 1994, Semiadi et al. 1994, Aagnes et al. 1996, Kim et al. 1996, Lechner et al. 2010), (e) tragulids and bovids (Hoppe 1977, Foose 1982, Pathak et al. 1992, Murray 1993, Bernard et al. 1994, Nolan et al. 1995, Maloiy & Clemens 1999, Shipley & Felicetti 2002, Thines et al. 2008), (f) camelids (Foose 1982, Gihad et al. 1989, Warmington et al. 1989, Cahill & McBride 1995, Lemosquet et al. 1996, Vernet et al. 1996, Dulphy et al. 1997a, Fraser & Baker 1998, López et al. 1998, López et al. 2001, Sponheimer et al. 2002, Cianci et al. 2004). The thick solid line represents the standard curve from Van Soest (1965) for sheep; thin lines represent the regression lines of the data for domestic sheep, goats, cattle, all cervids, large antelopes, and all camelids (cf. Table 1).

sheep (with only very narrow 95% CI overlap), indicating a less steep decline of intake with increasing dietary NDF (Table 1). The regression line for rhinoceros species was very similar to the 'sheep standard' (Fig. 7c). Sea cows had comparatively low intakes, as did hippopotamuses, whereas very high intakes were recorded in elephants (Fig. 7d).

Macropods generally had a lower intake than the 'sheep standard' (Fig. 8a), and no overlap existed between domestic sheep and all macropods or the red kangaroo *Macropus rufus* only (Table 1). However, 95% CI for *b* overlapped between these groups, indicating a similar pattern of decrease in intake with increasing dietary fibre (Table 1). Hindgut-fermenting marsupials generally had low food intakes (Fig. 8b).

The few measurements on forage diets in bears showed a similarity in the intake range of pandas *Ailurus spp.* and elephants (cf. Figs 7d and 9). Two individual measurements for grizzly bears *Ursus arcots horribilis* and black bears *Ursus americanus* lay on the 'sheep standard' (Fig. 9).

Lagomorphs showed a large variation in intake measurements, in which no decline with increasing forage fibre content was discernable (Fig. 10a). Guinea pigs *Cavia porcellus* and some other rodents had comparatively low food intakes, but again no trend was visible; only in tree porcupines *Erethizon dorsatum* was there a non-significant trend of decreasing food intake with increasing forage fibre content, at generally extremely low intake levels (Fig. 10b). In two vole species and pocket gophers, existing data indicated an increase in intake with increasing forage fibre content as mentioned before (Fig. 10c); compared to other species for which data on forages were available, the voles displayed particularly high food intakes.

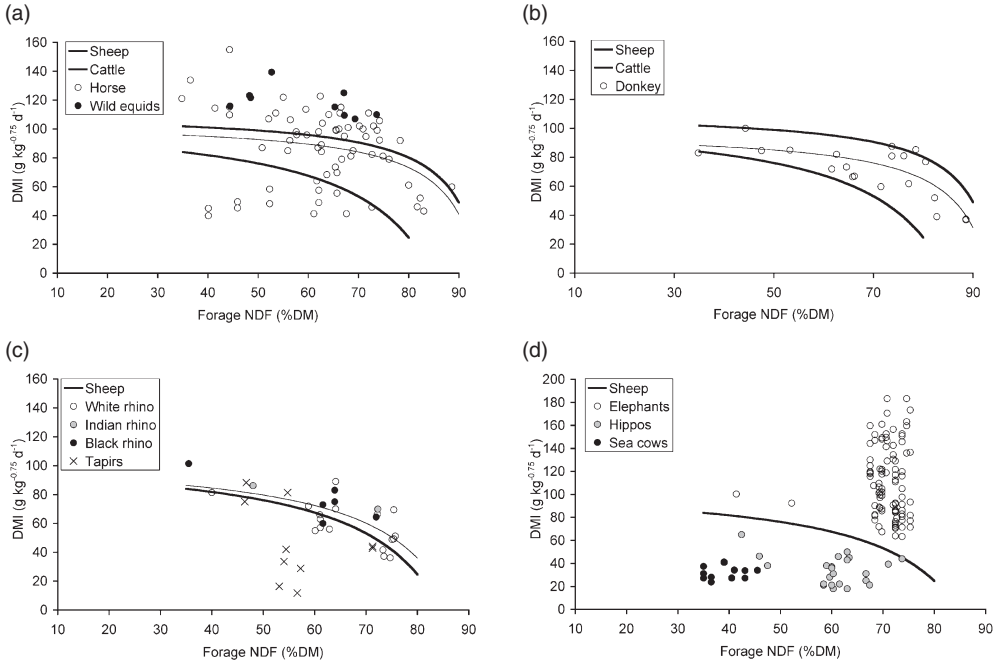


Fig. 7. Relationship between forage neutral detergent fibre (NDF) content and voluntary dry matter intake (DMI) in (a) domestic horses and wild equids (Haenlein et al. 1966, Foose 1982, Coenen 1986, Cymbaluk 1990, Pearson & Merritt 1991, Cuddeford et al. 1995, Crozier et al. 1997, Dulphy et al. 1997b, 1997c, Fehrle 1999, LaCasha et al. 1999, Pearson et al. 2001, Bergero et al. 2002, Sponheimer et al. 2002, Ordakowski-Burk et al. 2006, Pearson et al. 2006, Peiretti et al. 2006), (b) domestic donkeys (Izraely et al. 1989, Pearson & Merritt 1991, Mueller et al. 1994, 1998, Pearson et al. 2001, 2006, Smith et al. 2007), (c) rhinoceroses and tapirs (Foose 1982; Kiefer 2002; Steuer 2006, Lang-Deuerling 2008), (d) elephants, hippopotamuses and sirenians (Arman & Field 1973, Foose 1982, Lomolino & Ewel 1984, Hackenberger 1987, Roehrs et al. 1989, Aketa et al. 2003, Clauss et al. 2003, Goto et al. 2004, Schwarm et al. 2006, 2009). The lower thick solid line represents the standard curve from Van Soest (1965) for sheep and in (a) and (b) the upper solid line represents the curve for domestic cattle from this review; thin lines represent the regression lines of the data for domestic horses, domestic donkeys, and all rhinoceros species combined (cf. Table 1).

DISCUSSION

The most important finding of this review is the paucity of comparable data for most herbivores, in particular, smaller species. Whole forages are rarely used in trials with smaller herbivores. For large mammals, the available data confirm that some species have a strategy of high food intake (and low digestibility), in particular, elephants (Clauss et al. 2003) and pandas (Dierenfeld et al. 1982), and that certain groups such as the marsupials are characterized by comparatively low intakes (Munn et al. 2008). So far, elephants remain, to our knowledge, the only large herbivores in which an increase in food intake with declining diet quality has been demonstrated in the field (Meissner et al. 1990).

Apart from these differences in the general level of food intake (cf. differences in *a* in Table 1), relevant differences between herbivore groups are difficult to prove with existing data. Most notably, different responses to diet quality are difficult to prove between ruminants and perissodactyls in general, and between domestic

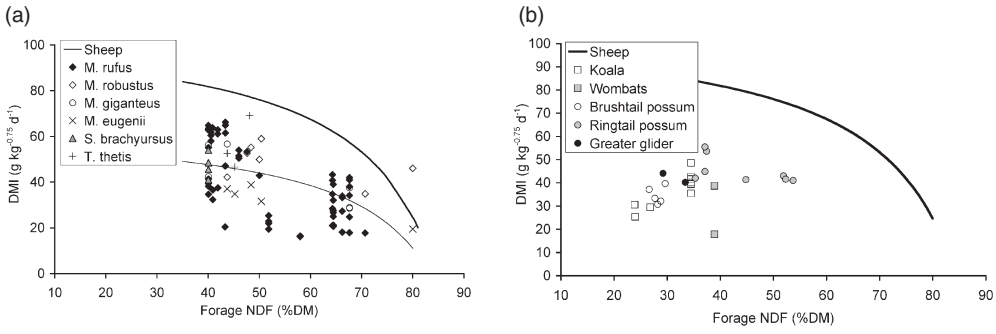


Fig. 8. Relationship between forage neutral detergent fibre (NDF) content and voluntary dry matter intake (DMI) in (a) macropods (Munn et al. 2008), (b) hindgut fermenting marsupials (Ullrey et al. 1981, Cork et al. 1983, Chilcott & Hume 1984, Foley 1987, Foley & Hume 1987, Barboza 1993, Hume et al. 1996). The thick solid line represents the standard curve from Van Soest (1965) for sheep; the thin line represents the regression line for all macropod species (cf. Table 1).

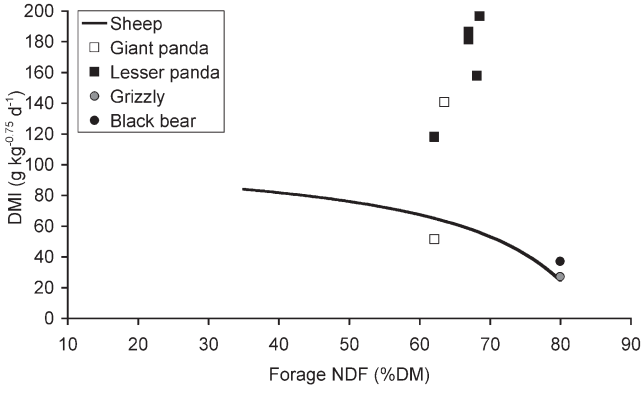


Fig. 9. Relationship between forage neutral detergent fibre (NDF) content and voluntary dry matter intake (DMI) in bears (Dierenfeld et al. 1982, Pritchard & Robbins 1990, Wei et al. 1999b, 1999a). The thick solid line represents the standard curve from Van Soest (1965) for sheep.

ruminants and horses in particular. Given the common acceptance of a difference between the latter two groups in the literature, this result is particularly surprising.

The main limitation of this review is our reliance on a single parameter to characterize diet quality – neutral detergent fibre. Although this measure is considered highly relevant in ruminants (Van Soest 1994, pp. 345–347), other authors found better correlations between intake and other parameters not available to us, for example *in vitro* digestibility (Meissner & Paulsmeier 1995). The large variation evident in most plots indicates that other factors must be important; on the part of the forage, these could, for example, comprise the lignification of fibre, or the contents of other nutrients such as protein, fat, sugars or starch – measures not available on a larger scale. Additionally, other physical properties might be important. For example, experience from captive animals indicates that forages usually accepted by grazers are less accepted by browsing species (Clauss & Dierenfeld 2008,

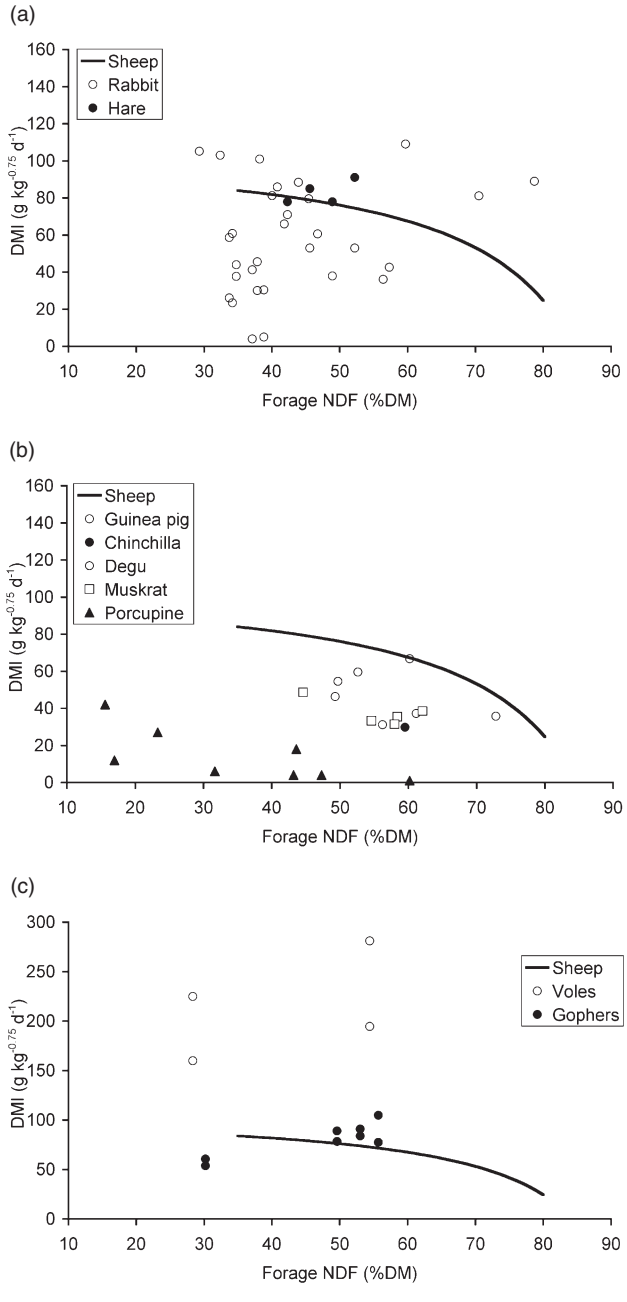


Fig. 10. Relationship between forage neutral detergent fibre (NDF) content and voluntary dry matter intake (DMI) in (a) lagomorphs (Monk 1989, Wenger 1997, García et al. 2000, Sponheimer et al. 2002, Kuijper et al. 2004, Thines et al. 2007), (b) rodents (Campbell & MacArthur 1994, Meyer et al. 1996, Wenger 1997, Kenagy et al. 1999, Felicetti et al. 2000), (c) voles and gophers (Loeb et al. 1991, Young Owl & Batzli 1998). The thick solid line represents the standard curve from Van Soest (1965) for sheep.

Clauss et al. 2008a), which might be a reason for the particularly low intakes recorded in some exotic small ruminants (Fig. 6e). However, this rule is not universal; for example, black rhinoceroses *Diceros bicornis*, although strict browsers in the wild, readily accept grass hay in captivity (Clauss & Hatt 2006). The provision of natural forages is even more problematic in captive primates (Clauss & Dierenfeld 2008), and it is not surprising that intake studies with primates on whole natural forages are absent from this data collation. Especially in browse leaves, secondary compounds might be more limiting for intake than fibre content, as demonstrated in koalas *Phascolarctos cinereus* (Lawler et al. 1998). Evidently, investigations more focussed on individual species should take the diversity of the plant food ingested more into account, e.g. differentiating between monocot and dicot forage (see, e.g. Edouard et al. 2008 discussed below). With respect to animal factors that could influence variance in the data, differences in physiological state (body condition, reproductive status, growth) are important (see below).

It must also be noted that the data on food composition used in this review are from the food as offered, not the food as ingested by the animals. Most animals, particularly small ones, consume forages in a selective manner, and the degree to which selective feeding is possible influences food intake and digestibility (e.g. Savadogo et al. 2000). However, it can be safely assumed that selective feeding would lead to lower fibre levels in the ingested diet, hence shifting data points given in Figs 6–11 somewhat to the left, and thus reinforcing rather than eliminating the observed patterns.

In particular, due to the widespread acceptance of the concept proposed by Janis (1976; see Introduction), research on the reaction of horses to diets of decreasing quality has been continuously common in the past. Laut et al. (1985) found an increase in intake when sawdust was added in increasing proportions to a compound feed otherwise based on grains. In contrast, when whole forages were assessed, many researchers demonstrated a negative effect of forage fibre level on food intake in domestic horses (Fonnesbeck et al. 1967, Darlington & Hershberger 1968, Foose 1982, Cymbaluk 1990, Crozier et al. 1997, LaCasha et al. 1999, Ordakowski-Burk et al. 2006, Pearson et al. 2006). Therefore, other authors have concluded that horses might respond to increasing forage fibre in a similar fashion as cattle (Dulphy et al. 1997c, Mesochina 2000) – an interpretation also backed by the results of this review (which draws largely on the same sources).

Direct comparisons in foraging patterns between horses and cows are rare; however, Arnold (1984) and Duncan et al. (1990) observed longer daily grazing times in horses than in cows or sheep, and Menard et al. (2002) observed a higher food intake in free-ranging horses than in cows in the same habitat. Unquantified observations indicate that when forage quality is very low, ruminants lose body condition but sympatric horses are less affected (Abaturov 2005, Koene 2006); and in South African game reserves, it is considered a sure indication of extreme drought or habitat deterioration if not only the wild ruminants, but also the zebras markedly lose condition (A. Shrader, pers. comm.). Nevertheless, experimental data that support these observations evidently remain to be produced.

With a large dataset not available to other researchers (reading data from graphs was not feasible for our review due to differences in the basis of intake measurements), Edouard et al. (2008) found conflicting results in horses. Intake declined slightly with decreasing forage quality when data from horse groups were analysed,

but increased with decreasing forage quality in a set of data for individual horses. Note, however, that in their analysis, different forage classes (grass hay, fresh forages and alfalfa hay) were considered separately, and that the graphs show that if all forages were combined, intake would decrease with increasing dietary fibre. These results indicate that effects should be investigated at finer scales, such as within certain forage types or plant communities that have ecological relevance, and not between all kinds of forages one can feed under experimental conditions. However, Edouard et al. (2008) also underline that the general reaction of horses towards declining diet quality does not correspond to the 'compensation theory' over a large range of forages. Notably, in the face of the more detailed analyses on the forage class and individual level, similar detailed analyses need to be performed with ruminants before the results in horses can be interpreted in a comparative way.

A major limitation of the data available so far is the heavy reliance on experiments with domesticated species. Edouard et al. (2008) commented on the relevance of human selection on specific traits in domestic animals. Whereas selection for high production will have increased food intake capacities in ruminants (Forbes 2007), such selection is unlikely to have occurred in horses; in contrast, the practice of feeding horses with concentrates might even have reduced their intake capacity. The limited available data show that whereas wild cattle, sheep and goats have intakes at the lower range of their domestic counterparts (Fig. 6a–c), the opposite is true for horses (Fig. 7a). Therefore, differences between ruminants and equids might be more pronounced in wild than in domestic species. Evidently, especially more data on wild equid species are needed.

In addition, a systematic difference in the reproductive state of the cattle and horses used in intake experiments probably had a major influence on the intake level: often, measurements were performed on cattle in different stages of growth or lactation and hence at energy requirements above maintenance, whereas horses were more often assessed under maintenance conditions. For example, Pearson et al. (2006) explained their finding that intake was similar in cattle and ponies by the fact that the cattle of their study were still growing, whereas the ponies were not. Note, however, that the large majority of data on sheep and cattle we used were derived from Reid et al. (1988), who used mature, non-lactating animals.

However, even if some data from cattle may not be representative of maintenance intake, they nevertheless do suggest that a mechanical limit to food intake, as postulated for ruminants by Janis (1976) and included in concepts of food intake limitation in domestic ruminants, may be less important than other digestive strategies. Note that even domestic cattle do operate with a typical ruminant digestive system, which evidently has evolved during domestication to facilitate high food intake levels. Constraints other than mechanical factors should probably be considered first when comparing different digestive strategies. For example, non-ruminant foregut fermenters do not operate a sorting mechanism, i.e. they do not have a mechanical rate-limiting step involving forestomach clearance. Nevertheless, they generally operate at lower food intake levels than ruminants (Clauss et al. 2007, Schwarm et al. 2009, Clauss et al. 2010), and equids, whose digestive tract contains two distinct anatomical 'bottleneck' structures, have generally higher food intakes than rhinoceroses (Fig. 7a,c), which do not have these structures (Clauss et al. 2008c).

The comparison of the data for rhinoceroses and tapirs (Fig. 7c) with those for horses and ruminants indicates an important addition to the conventional concept of

'low intake in ruminants vs. high intake in hindgut fermenters': even if hindgut fermenters do have the potential to adopt a high-intake strategy, as in equids and elephants, there is no reason inherent in their digestive physiology why they would have to do so. Actually, the hindgut fermenter-system allows a variety of intake strategies, ranging from very low to very high intake ranges; in contrast, foregut fermenters appear limited to the low end of the intake range spectrum. Rumination is the key innovation that allows (but again does not oblige) foregut fermenters to expand their intake into the higher range (Clauss et al. 2008b, Schwarm et al. 2009, Clauss et al. 2010). Among the large herbivores, the rhinoceros species are good examples of hindgut fermenters without high food intakes. In competing with ruminants for resources, rhinos probably rely on other adaptations than those of the digestive tract.

The duration of the experiments, which is often overlooked, is probably the most important factor influencing the patterns observed in our dataset. The digestive strategies of all herbivores have evolved in response to predictable or unpredictable patterns of change in food availability and quality. This is most evident in the coupling of life histories to a seasonal cycle in temperate species, and in the readiness to adapt to unforeseen events in subtropical species (Barboza & Hume 2006, Clauss et al. 2010). Any feeding trial in which forage quality is manipulated therefore represents a dietary signal similar to seasonal or aseasonal variation (while other signals, such as photoperiod or climate, possibly remain constant). The response of the animal to this signal is not only an adaptation of food intake level according to its digestive strategy, but also according to its organismal strategy to deal with seasonal or aseasonal variation in habitat quality.

One important aspect of the organismal strategy is the body condition of the animal at the beginning of the decline in diet quality. Studies in sheep (Foot 1972, Sibbald & Kerr 1994, Sibbald 1997, Sibbald & Rhind 1997, Tolkamp et al. 2006) and cattle (Bines et al. 1969) demonstrated that voluntary food intake is higher in animals with reduced body stores. Differences in body condition can also influence dietary preferences, increasing the range of forages accepted by thinner animals (Pfister et al. 2008). Similarly, Edouard et al. (2008) showed in horses that some individuals exceeded their maintenance requirement on a low-fibre forage but decreased their food intake to meet requirements on a high-fibre forage, whereas other individuals ate close to maintenance requirements on low-fibre forage, but increased their intake to remain at maintenance requirement on high-fibre forage.

The general decline in food intake with diet quality in many species can be parsimoniously interpreted as part of the organismal strategy to deal with variation in forage quality. Rather than regulating food intake in synchrony with diet quality, i.e. compensating instantaneously for low diet quality by increasing the momentary food intake, herbivores may opt for the anticipatory strategy of increasing food intake on high quality food, building up energy reserves for periods of lower food quality (Barboza & Hume 2006). Such seasonal strategies have not only been demonstrated in many ruminant species (Clauss et al. 2010) but also in the hindgut fermenters Przewalski horse *Equus ferus przewalskii* (Arnold et al. 2006, Kuntz et al. 2006) and white rhinoceros *Ceratotherium simum* (Shrader et al. 2006). An intriguing question is: by which mechanisms, and for what reasons, do animals adjust their intake on lower-quality forage to the observed lower levels?

For data from short-term experiments, such as the data collated for this review, these considerations have the evident consequence that responses to a diet of lower quality might be tempered by the fact that most experimental animals were probably in good condition, and hence were not actually challenged to increase food intake. These considerations lead to the question: what duration should be considered adequate for food intake experiments aimed at discerning differences in the intake capacity between different species or digestive systems? In theory, differences in the ability to ingest low quality diets should become evident once animals have depleted their body fat stores and rely on food intake alone for maintenance energy. However, long-term studies on comparative food intake in horses or cattle, for example, are lacking. Such longer experimental periods might also facilitate higher intakes on lower-quality forage by allowing an adaptation of the digestive tract. Increasing capacities of the digestive tract (both in terms of an increase in volume and tissue) in response to declines in diet quality have been reported in numerous rodent species (reviewed in Karasov & McWilliams 2005, Naya et al. 2008) and also in large herbivores (e.g. Weckerly 1989).

The species' ability to endure fasting may be an important determinant of the adaptation time required to achieve results that actually reflect characteristics of its digestive system. Fasting endurance is linked to body mass – larger animals are able to endure longer fasts (Lindstedt & Boyce 1985, Millar & Hickling 1990, Barboza & Hume 2006). In addition to having a strategy of accreting body reserves, larger animals are also likely to adopt a strategy of migration to ensure high forage quality (Fryxell & Sinclair 1988), whereas smaller animals are mostly unable to evade their habitat in times of lower food quality. With respect to their reaction to an experimental reduction in forage quality, this could translate into an anticipatory response (reducing intake with decreasing forage quality) in larger animals, which simply 'sit out' the experimental period of lower forage quality, but in an instantaneous response (increasing intake with declining forage quality) in smaller herbivores. Although data on small herbivores are mostly lacking, data from two studies on very small rodents show the expected pattern (Fig. 10c).

In theory, herbivores that separate nutrient-rich ingesta from indigestible components in a colonic separation mechanism and recycle this nutrient-rich material via coprophagy (Hume & Sakaguchi 1991) should be particularly adapted to a response of instantaneously compensating food intake. If we assume that metabolic losses, in particular microbial protein, are related to dry matter throughput through the fermentation chamber, and that low-quality forage itself does not stimulate compensatory microbial growth, then increasing food intake with declining forage quality does not appear to be a logical option for a herbivore below a certain quality threshold. Actually, such a hypothetical trade-off between the stimulation of microbial growth and the causing of metabolic losses represents the most likely reason for the reduced food intake observed in many herbivores on lower-quality forages, and represents one of the most promising areas of future herbivore research. However, if faecal losses of microbial protein can be countered by separating and re-ingesting bacterial protein, an increased intake of low-quality forage appears feasible. Although the available data appear to be too few to allow a generalization in this respect, these considerations add an important aspect to the body size limitation observed in the strategy of coprophagy. The colonic separation mechanism, and the strategy of coprophagy, apparently does

not occur in herbivores larger than capybaras *Hydrochoerus hydrochaeris* (*c.* 40kg; Hirakawa 2001, 2002). One potential reason for this size limit could be mechanical limits to the colonic separation mechanism at increasing body sizes and hence colon diameters. Another reason could be that at larger body sizes, animals might use strategies other than direct digestive strategies to deal with increased metabolic losses at high intakes of low-quality forages – for example, an anticipatory food intake pattern with a reliance on body stores in times of low forage quality.

In conclusion, our review demonstrates that differences in the reaction to variation in forage quality mostly remain to be investigated – either in a specific ecological context which allows for differences in the reaction to seasonal or aseasonal variation via differences in the acquisition of body reserves and energy saving mechanisms such as torpor or hibernation, or in a specific physiological context which allows the definition of differences between digestive strategies without the confounding effects of body reserves or energy saving. The existing data suggest that a major difference between foregut and hindgut fermenters is the range of food intake possible: whereas foregut fermenters are limited to generally lower food intakes (and ruminants are at the higher end of the foregut fermenters' range), hindgut fermentation allows a broader spectrum of relative food intakes, from the very low intakes observed in some marsupials, to the intermediate intake levels observed in rhinoceroses, to the very high food intakes observed in elephants.

Differences in the pattern by which herbivores react to variation in forage quality, however, can so far not be conclusively stated for the different digestion types. When the equations of Table 1 are used to express the decline in food intake with increasing forage fibre content on a relative basis (in % of initial food intake), it appears that domestic cattle, horses and donkeys share a common pattern, and sheep, wild ruminants, camelids, hippos and rhinos another common pattern (Fig. 11). Notably, both foregut and hindgut fermenters are represented in both groups. In contrast to in previous concepts, macropods rank lowest, suggesting a particular susceptibility to a decrease in intake at declining forage quality. However,

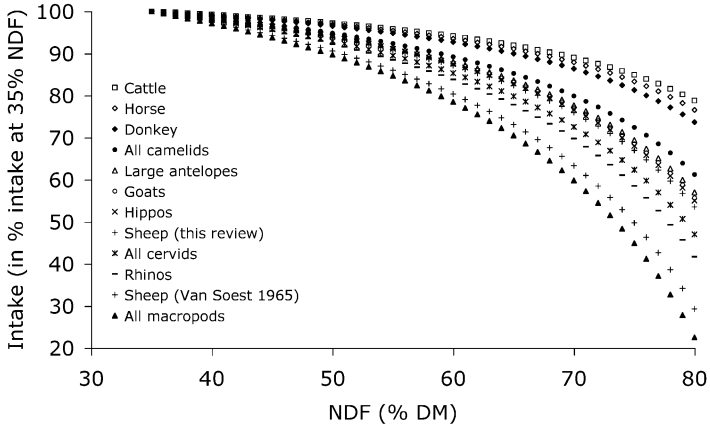


Fig. 11. Relationship of forage neutral detergent fibre (NDF) content and the reduction in food intake when expressed as % of the assumed initial intake of a forage with an NDF content of 35%. Intake is calculated from equations in Table 1. Note that although differences appear evident, overlap of confidence intervals in Table 1 do not allow conclusive interpretation.

given the large overlap of confidence intervals in Table 1, these results should only be considered hypotheses that need to be tested in controlled future studies.

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